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Original Article

Identifying juvenile and sub-adult movements to inform recovery strategies for a high value fishery—European bass (*Dicentrarchus labrax*)

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The European bass (*Dicentrarchus labrax*) support high value commercial and recreational fisheries, however the Spawning Stock Biomass (SSB) of the northern Atlantic stock (ICES divisions 4.b–c, 7.a, and 7.d–h) has rapidly declined to an unsustainable level. The decline in SSB has been attributed to high fishing pressure combined with poor recruitment. By tracking juvenile fish their spatial ecology can be identified, and appropriate fisheries management policies designed to boost recruitment can be implemented. Using acoustic telemetry 146 sub-adult European bass (25.2–60 cm fork length) were tracked for up to 370 d across three sites in the southwest of the UK. Tagged fish were detected 2 724 548 times (Range: 166–106 393 detections per fish). Linear modelling estimated tagged fish were resident within 2.4–20.1 km of the site where they were first caught for 42.9–75.5% of the year. Some fish were however resident throughout summer and winter. Individual fish were also tracked moving up to 317 km to other coastal sites, 81% of which returned to their original capture site. Fisheries management should account for the high site fidelity displayed by juveniles and sub-adults of this species and coastal nursery sites should be considered essential habitat.

Keywords: acoustic telemetry, essential fish habitat, fish residency, good environmental status, movement

Introduction

The European bass (*Dicentrarchus labrax*) is a commercially and recreationally important finfish native to the Northeast Atlantic and Mediterranean Sea (Pickett and Pawson, 1994). The species is targeted throughout its range, with commercial and recreational fisheries worth an estimated £56 million & £172 million per year, respectively (EUMOFA, 2020). The commercial fishery varies between countries, however landings are typically highest in the North Sea, English Channel, and Bay of Biscay (EUMOFA, 2020; MMO, 2020). In particular, this species is important for inshore fishing fleets (vessels < 12 m length), in countries such as Belgium, France, Netherlands, Spain, and the UK accounting for an estimated 13–63% of finfish landings (EUMOFA, 2020; MMO, 2020).

In 2010, the International Council for Exploration of the Seas (ICES) reported a dramatic decline in the Northern stock (ICES divisions 4.b–c, 7.a, and 7.d–h), which in 2016 declined below “safe biological limits,” a threshold known as B_{lim}. Due to strict conservation measures, in 2019 the Northern stock increased above B_{lim}, however relative to historic levels the population remains in a highly impoverished state and is still below maximum sustainable yield thresholds (ICES, 2020). The decline in the Northern stock is thought to be the result of several concomitant issues such as, unsustainable fishing pressure combined with poor recruitment (ICES, 2020). However, when these are combined with life history characteristics such as slow growth rates (Pickett and Pawson, 1994), recovery timeframes are likely to be protracted.

Limited research has been conducted on juvenile or sub-adult fish (< 42 cm total length) which, relative to sexually mature conspecifics, are thought to spend a high proportion of time within coastal and/or estuarine nursery areas (Pawson *et al.*, 1987; Kelley, 1988; Pickett and Pawson, 1994; Pickett *et al.*, 2004). Recruitment from these nursery habitats are thought to replenish the sexually mature population (Pickett *et al.*, 2004), therefore management or conservation efforts that are targeted at increasing juvenile fish populations are likely to be highly beneficial for recovery efforts (Pickett *et al.*, 2004).

Environmental conditions e.g. water temperature, and anthropogenic stressors e.g. fishing pressure or coastal land-use practices, are thought to highly influence juvenile bass populations (Laffaille *et al.*, 2000; Green *et al.*, 2012), causing variability in growth rates (Ying *et al.*, 2011; Wright *et al.*, 2019), and abundance (Wright *et al.*, 2019, 2020). There however remains a lack of understanding on how juvenile bass populations exploit inshore areas, or their associated spatial ecology. This evidence could therefore be used to design and then implement fisheries management policies, which maximize recruitment rates from coastal nursery sites (Pickett *et al.*, 2004).

Due to the knowledge gaps in juvenile European bass spatial ecology, and the potential benefits to help recovery efforts, this study will use a regional acoustic telemetry network to (1) quantify juvenile and sub-adult European bass site fidelity and residency to three coastal sites within the southwest of the UK; (2) test how this varies between sites and with fork length; and (3) estimate how far tagged fish disperse along the open coastline from the site where they were caught, tagged, and released.

Material and methods

Nursery sites

European bass were tracked across the Southwest of the UK with a focus on three designated nursery sites (MAFF, 1990): The Dart estuary, Salcombe harbour, and the Taw/Torridge estuaries (Figure 1 and Table 1). All sites host a range of intertidal and subtidal sediment habitats and tidally-swept rocky reefs. These sites are also designated as protected as Bass Nursery Areas (MAFF, 1990), and local fisheries bylaws prohibit commercial netting activities (D&S IFCA, 2018).

Tagging procedure

From June to August 2018, 146 European bass were captured by rod and line via commercial and recreational anglers using soft lures. A minimum weight threshold of 120 g was used, to ensure the tag weight burden did not exceed 3.5% of the fish weight, which has previously been demonstrated as a suitable for this species (Lefrancois *et al.,* 2001, Bégout Anras *et al.,* 2003). Each fish was anaesthetized with an induction dose of 70–100 mg/l MS-222 (Tricaine methanesulfonate). Fish were then positioned dorsally on a V-shaped cradle, where they were ram-ventilated with a maintenance anaesthetic dose of 30–40 mg/l MS-222. Induction and maintenance anaesthetic varied on an individual fish basis to ensure the required depth of anaesthesia was achieved and maintained. A single 69 KHz Innovasea V92X transmitter tag (tag dimensions: 29 × 9 mm, 4.7 g—air weight) was implanted within the peritoneal cavity via a small incision (10–15 mm) made slightly off the mid-ventral line between the pelvic fin and anus. Transmitter tags were programmed to emit a randomized uniquely-coded ping once every 80–160 s. Following tag implantation, the surgical site was closed using dissolvable sutures and/or medical grade adhesive. Analgesic was topically applied to the surgical site (Lidocaine 1% solution diluted to 1:10 with NaCl saline solution). Fish were then monitored within large holding tanks (500 l) for a minimum period of 1 h prior to release as close to the capture site as logistically possible. All tagging procedures were conducted under a UK Home Office license (P81730EA5) by personal license holders with PILC entitlement. Dispensation was also provided by the relevant regulatory and land authorities.

Acoustic telemetry receiver array

A total of 78 Innovasea VR2W and VR2Tx receivers were deployed (Figure 1 and Table 1) across three designated nursery sites: The Dart, Salcombe harbour, and the Taw/Torridge estuaries. Different receivers models (VR2W and VR2Tx) were deployed for logistical reasons, and no distinction was made between these during data analysis.

The receiver configurations consisted of a series of detection gates that spanned the mouth of each site up to the mean tidal limit. Receiver gates had a mean spacing of 0.9 km (± 0.09), 0.82 km (± 0.4), and 1.8 km (± 1.6) for the Dart estuary, Salcombe harbour, and the Taw/Torridge estuaries respectively. These were opportunistically attached to existing structures e.g. channel marker or moorings. Upon successful detection of each tagged fish; the time, date and tag ID was recorded on each receiver. This was periodically downloaded every 3 months throughout the study.

Range testing

A V9 range test tag, with comparable power output to those implanted within the fish, was deployed in a linear array of six receivers in Salcombe harbour. Receivers were spaced approximately 150 m apart (Annex 1, Figure 10) and deployed for a 2 week period at the start of the study. The number of successful detections at varying distances from the range test tag were summarized.

Data analysis methods

All data manipulation and statistical analysis was conducted using R version 3.6.0 (R Core Team, 2019).

Overall fish detection trends

Detection records were presented in an abacus plot with tag ID arranged on the *y*-axis by fork length and binned into size/maturation classes. This enabled visualization of broad scale patterns of presence/absence within each nursery site and how this varied in relation to size/maturation. Size/maturation classes were defined by Pickett and Pawson (1994), based on examination of gonads of more than 2000 European bass:

- < 29 cm fork length/32 cm total length: Gonads immature—Juvenile.

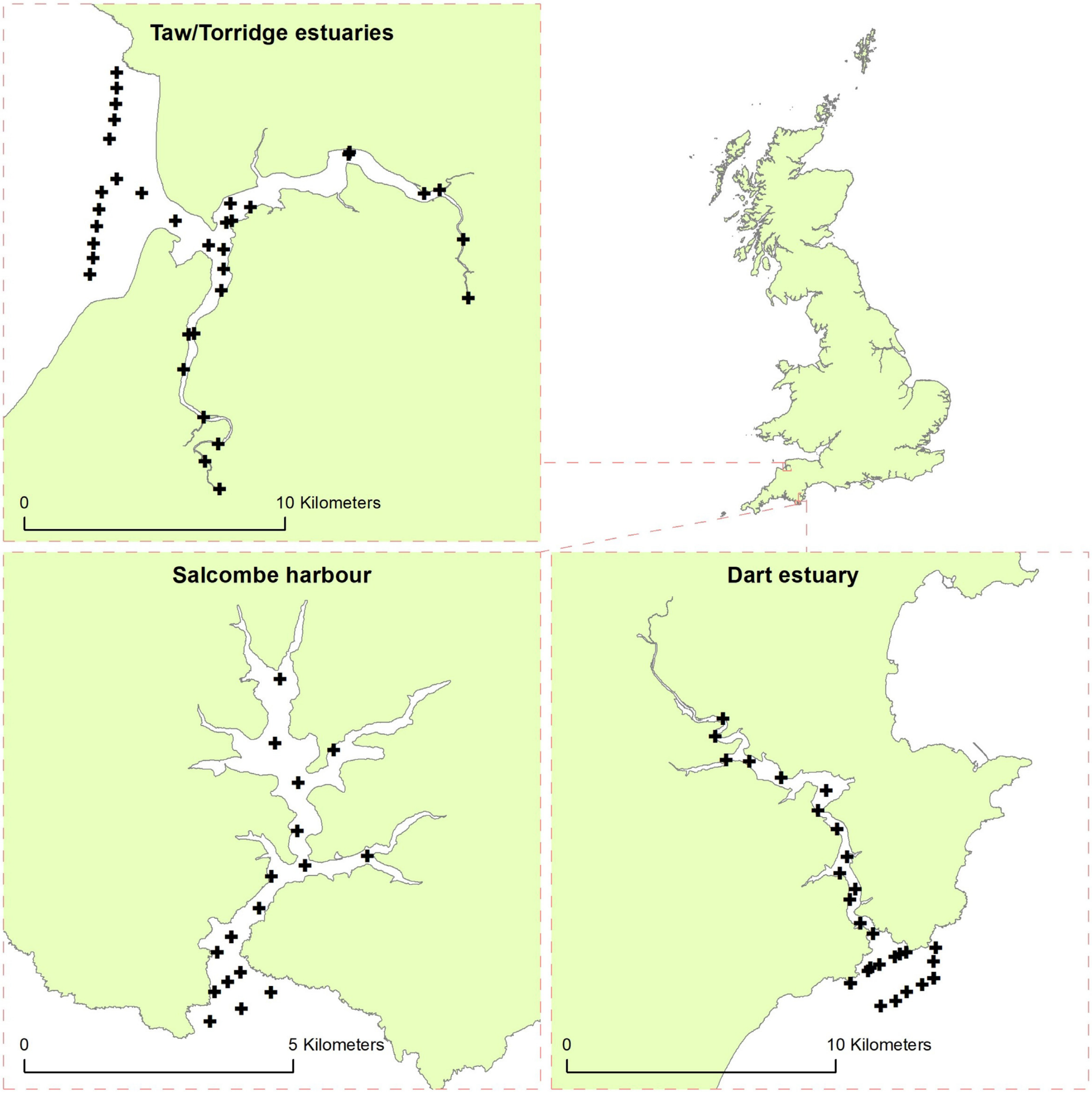

Figure 1. Acoustic telemetry array within the Taw Torridge estuary (top left), Dart estuary (bottom right), and Salcombe harbour (bottom left). Black cross hairs represent position of acoustic receiver. Please note map scales differ between sample sites.

Table 1. Physical characteristics of the nursery sites, area and centroid coordinates.

Nursery site	Waterbody type	Area (km^2)	Number of receivers	Deployment date	Latitude	Longitude
Dart estuary	Estuary[1]	8.32	28	22/08/2018	50.3822	−3.6061
Salcombe harbour	Ria	6.34	17	19/06/2018	50.2377	−3.7554
Taw/Torridge estuaries	Estuary	14.6	33	19/07/2018	51.0536	−4.1504

[1]The Dart estuary is technically defined as a ria system, however still has significant freshwater input via the river Dart

- 29–39.25 cm fork length/32–42 cm total length: Many males but very few females are found to have maturing gonads during winter and spring—Adolescent.
- > 39.25 cm fork length/> 42cm total length: fully mature or spent gonads during or after spawning period (February–July)—Adult.

Characterizing fish residency and movement characteristics

Subsequent data analysis then focussed on periods of "residence" and "absence" of each tagged fish within their respective nursery site. Filters were applied to the acoustic telemetry data to identify periods of time when fish were within each site, this was referred to as a residence period (Campbell *et al.*, 2012). A residence period began when a fish was detected by any receiver within each nursery site, and terminated when either a fish was detected in a different nursery site or was not detected for a period of 6 h (Doyle *et al.*, 2017). An absence period was defined by the termination of a residence period and the start of the proceeding residence period i.e. the period of time between residence periods.

Classifying absence period characteristics

Absence periods varied widely in their duration, the PELT-TREE classification method (Madon and Hingrat, 2014) was therefore used to assign the following broad behaviours to absence period of different lengths:

Wider movement (WM): defined by relatively "large" absence periods, which could happen as a result of fish conducting spawning migrations (October–April: Pickett and Pawson, 1994; Doyle *et al.*, 2017; Pontual *et al.*, 2019) or making wider movements along the coast (Pickett and Pawson, 1994).

Coastal movement: defined by a high frequency of absence periods with a low duration, during which fish were not thought capable of travelling far from the nursery site they were caught, tagged, and released. The total duration of time fish exhibited coastal movement was combined with the total duration of all residence periods. This provided an estimate of how long each fish was either within or in close proximity to the host nursery site throughout the tracking period. This was defined as Tagging Site Residence (TSR; **Figure 2**).

This was achieved using the following process:

1) Time series were constructed for each fish detailing the duration of each absence period throughout the tracking period (Figure 2).
2) Change point detection was used to break each time series into "segments" of time where there was a significant relative change in the mean duration of absence periods (R package "changepoint"—Killick and Eckley, 2014).
3) A supervised regression tree was then used to determine splitting rules for time series segments to identify when a fish was displaying "wider movement" or "coastal movement." An initial supervised "training" regression tree was created using 267 segments from 14 individuals (10% of tagged fish; R package "tree"—Ripley, 2019). Each segment within the training regression tree, was then manually assigned to either "Coastal Movement" or "Wider Movement."
4) Splitting rules for these different behaviours were derived from the training regression tree and then applied to the remaining dataset.

Wider movement

The timing and duration of segments identified as "wider movement," as well as the number of fish, which returned to their host nursery site following "wider movement" were qualitatively described.

Tagging site residence

To account for differences in the duration of time each fish was tracked (referred to as the tracking period) Tagging Site Residence (TSR) was converted to a percentage of the tracking period for each fish. A linear model implemented in "stats" (R Core Team, 2019) was then used to model TSR as a function of fork length, nursery site and the interaction between them. Model simplification was conducted using Akaike Information Criterion (AIC). Following the rules of parsimony the model with lowest AIC score was selected. If delta AIC scores from models were ≤ 2 the simplest model and/or that with the fewest fixed effects was selected (Zuur *et al.*, 2013). Statistical assumptions were visually assessed via model diagnostic plots. Tukey pairwise comparison implemented within "stats" (R Core Team, 2019) was used to assess at which nursery sites TSR significantly differed.

Estimating dispersal distances

When tagged fish that were detected in locations other than the nursery site in which they were tagged, Rate of Movement (ROM) was estimated using the straight-line distance (avoiding land) between receivers. ROM was not calculated from movement within each nursery site due to local tidal currents creating extreme (11 m/s) and variable flows, which could greatly influence ROM calculations for individual fish. To make the results from the current study broadly applicable, the average ROM of each individual fish were combined with those derived from O'Neill (2017). O'Neill (2017) also used acoustic telemetry to study European bass movement within coastal sites in southeast Ireland. The receivers within the current study and those within O'Neill (2017) were deployed in a similar design, however O'Neill (2017) focussed on sexually mature fish (>42 cm total length).

A Generalized Linear Model (GLM) with a Gaussian error structure and log link function was used to test a relationship between average individual ROM and fork length (R package "stats"; R Core Team, 2019). This linear relationship provided size-specific ROM estimates for European bass within the open coast from 26.2 to 71.4 cm fork length. This relationship was used to calculate the estimated range fish achieved during individual absence periods (estimate range = ROM $*$ duration of absence period).

A Linear Mixed Model (LMM) implemented in "nlme" (Pinheiro *et al.*, 2019) was then used to model the potential dispersal distance of tagged fish during TSR, using their estimated range (m) as a function of fork length, nursery site and the interaction between them. Within-individual replication was accounted for using tag ID as a random intercept term. Temporal autocorrelation was visually detected within the standardized model residuals via an autocorrelation plot (R Core Team, 2019). An autoregressive process order 1 (AR1) was therefore used to account for temporal dependency within the model correlation structure

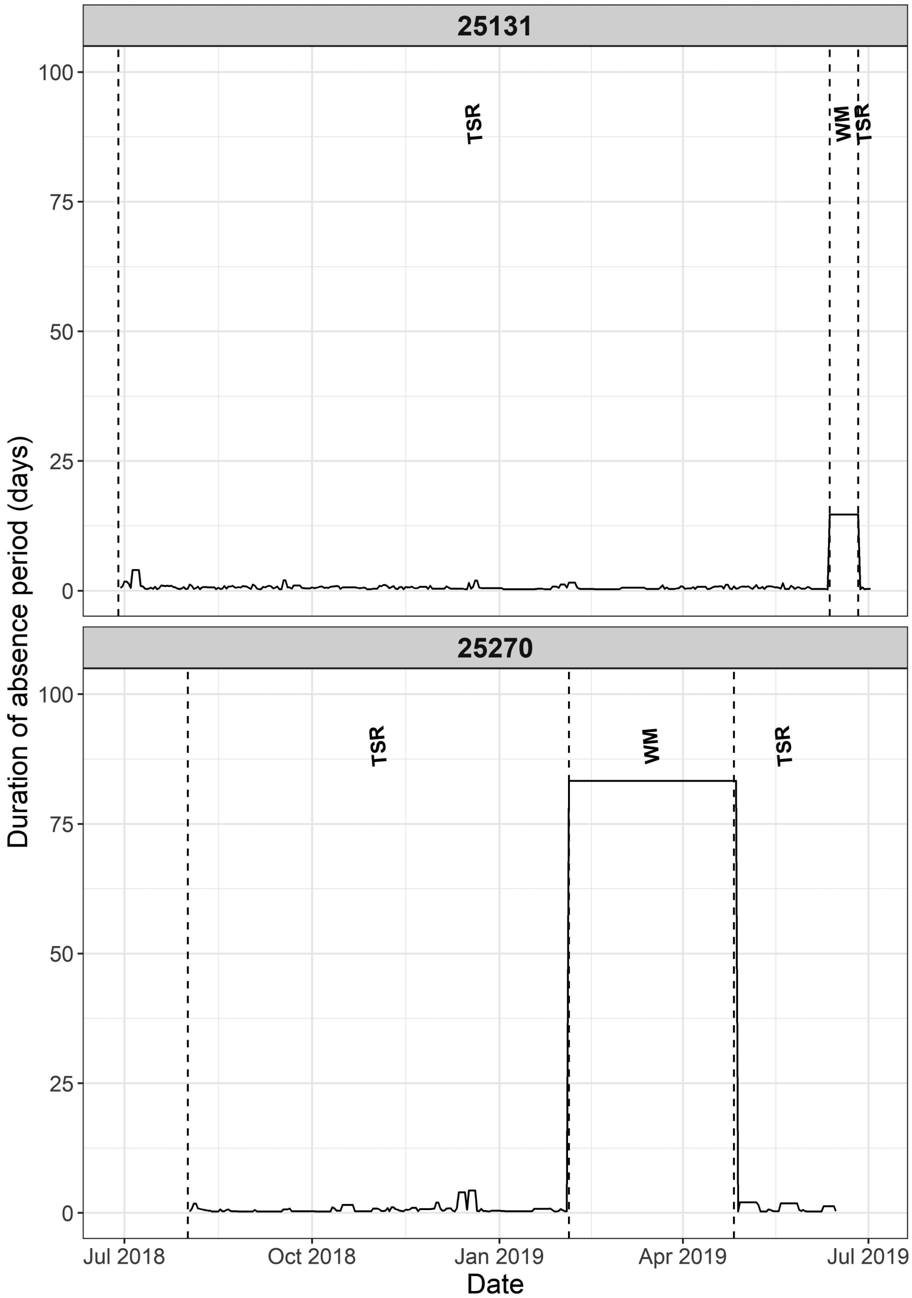

Figure 2. Absence period time series for tag ID 25131 (top) and 25270 (bottom), with segments identified as "Tagging Site Residence" (TSR) and "Wider Movement" (WM). Both fish were tagged within nursery site Salcombe harbour.

(Zuur *et al.*, 2013). AIC-based model simplification was then performed as outlined above to identify the most parsimonious combination of fixed effects. Statistical assumptions were visually assessed using model diagnostic plots. To demonstrate the spatial extent of predicted fish dispersal from each nursery site, a spatial buffer was created using model coefficients and 95% confidence intervals (95% *CI*) from the outermost/most seaward positioned receiver and presented in a map.

Results

A total of 146 fish were tagged as part of the study (Annex 1, Table 7; Dart estuary—51; Salcombe harbour—46; and Taw/Torridge estuary—49). Fish length ranged from 25.2 to 60 cm (fork length), with a mean of 33.5 cm (range: 26–52), 30.9 cm (range: 25.4–38.3), and 30.3 cm (range: 25.2–60) within the Dart estuary, Salcombe harbour, and the Taw/Torridge estuaries, respectively (Figure 3). A total of 90% (131 individuals) of the fish tagged were less than the Minimum Conversation Reference Size (MCRS; 39.25 cm fork length/42 cm total length), and where therefore assumed to be juvenile or sub-adult fish. The remaining 10% (15 individuals) were above the MCRS, and where assumed to be sexually mature fish. These fish were retained within the study due to logistical constraints limiting further fish capture, as well as allowing further study into variability of European bass residency with increasing fish size/maturation.

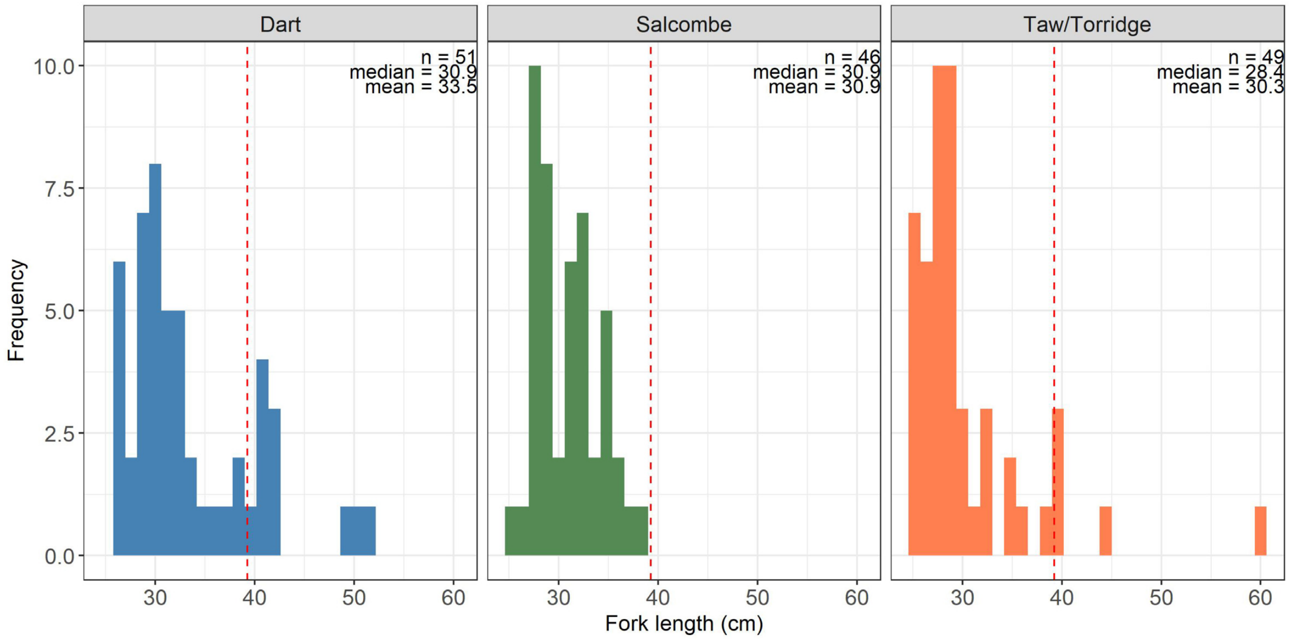

Figure 3. Size distribution of tagged European bass captured within the Dart estuary, Salcombe harbour, and the Taw/Torridge estuaries. Dashed line represents minimum conservation reference size: 39.25 cm fork length/42 cm total length.

No immediate mortality occurred as a result of the tagging procedure, however, 12 fish were not detected >30 d post-tagging, these were removed from further analyses.

Range testing

Range testing confirmed 60% ping detection at a range of 175 m. The channel width of each tagging site rarely exceeds 300 m, therefore by positioning receivers at central locations within each channel detection of tagged fish was assumed to be reliable.

Overall fish detection trends

Across all receivers, tagged fish were detected 2 724 548 times during the tracking period (Dart estuary—324 d; Salcombe harbour—370 d; and Taw/Torridge estuaries—346 d). The mean number of detections per fish was 19 053 with a range of 166–106 393. Detection were highest within Salcombe harbour (1 418 688), second highest within the Dart estuary (848 917), and lowest within the Taw/Torridge estuaries (393 943).

Seasonal differences in tagged fish detections were visually apparent between nursery sites (Figure 4). Fish tagged within the Dart estuary were detected regularly from August 2018 to January 2019. From January to April 2019, tagged fish were largely absent from the Dart estuary, however nine of the 51 fish tagged in the Dart were detected in Salcombe harbour during this period (mean length: 31.38 cm, range: 28.2–41.1 cm; Figure 4). From May 2019, tagged fish were detected regularly within the Dart estuary until the end of the tracking period. Fish tagged in Salcombe harbour were detected regularly throughout the tracking period (including winter). From August 2018 to January 2019 and June to July 2019, eight fish from Salcombe harbour were intermittently detected within the Dart estuary (mean length: 30.73 cm, range: 27.5–33.2 cm). The majority of fish tagged in the Taw/Torridge estuary were detected regularly, however six fish were absent from December 2018 to May 2019. From May to June 2019, two fish tagged in the Dart estuary were detected in Salcombe harbour and then in the Taw/Torridge estuary (fork length: 28.2 and 29.8 cm).

PELT-TREE classification

From the absence period time series, 1 784 unique segments were identified using the PELT change point detection method. On average 12.41 (Range: 2–36, IQR: 6.75–16) change points were detected for each tagged fish. The training regression tree had a residual mean deviance of 0.094 and a misclassification rate of 0.019. The training regression tree was able to define the following splitting rules:

- The first node of the tree split segments into absence periods identified as "Coastal movement" with mean duration < 5.6 d.
- The second node of the tree split segments into absence periods identified as "Wider movement" with a mean duration > 5.6 d.

Therefore, during segments of time identified through the PELT algorithm, in which the mean duration of absence period was less than 5.6 d tagged fish were determined to be displaying "Coastal movement." During segments when the mean duration of absence periods exceeded 5.6 d, tagged fish were determined to be displaying "Wider movement."

Wider movement

All tagged fish conducted wider movements, during which absence periods had an average duration of 23.2 d (Range: 4.7–243.5 d, IQR: 7–20.5).

As a result of the seasonal timing and long duration of some absence periods, 60 out of 133 (45%) tagged fish were suspected of either conducting spawning migrations or moving out of their respective nursery site during the winter (Pickett and Pawson, 1994) (Dart estuary—34, Salcombe harbour—nine, and Taw/Torridge

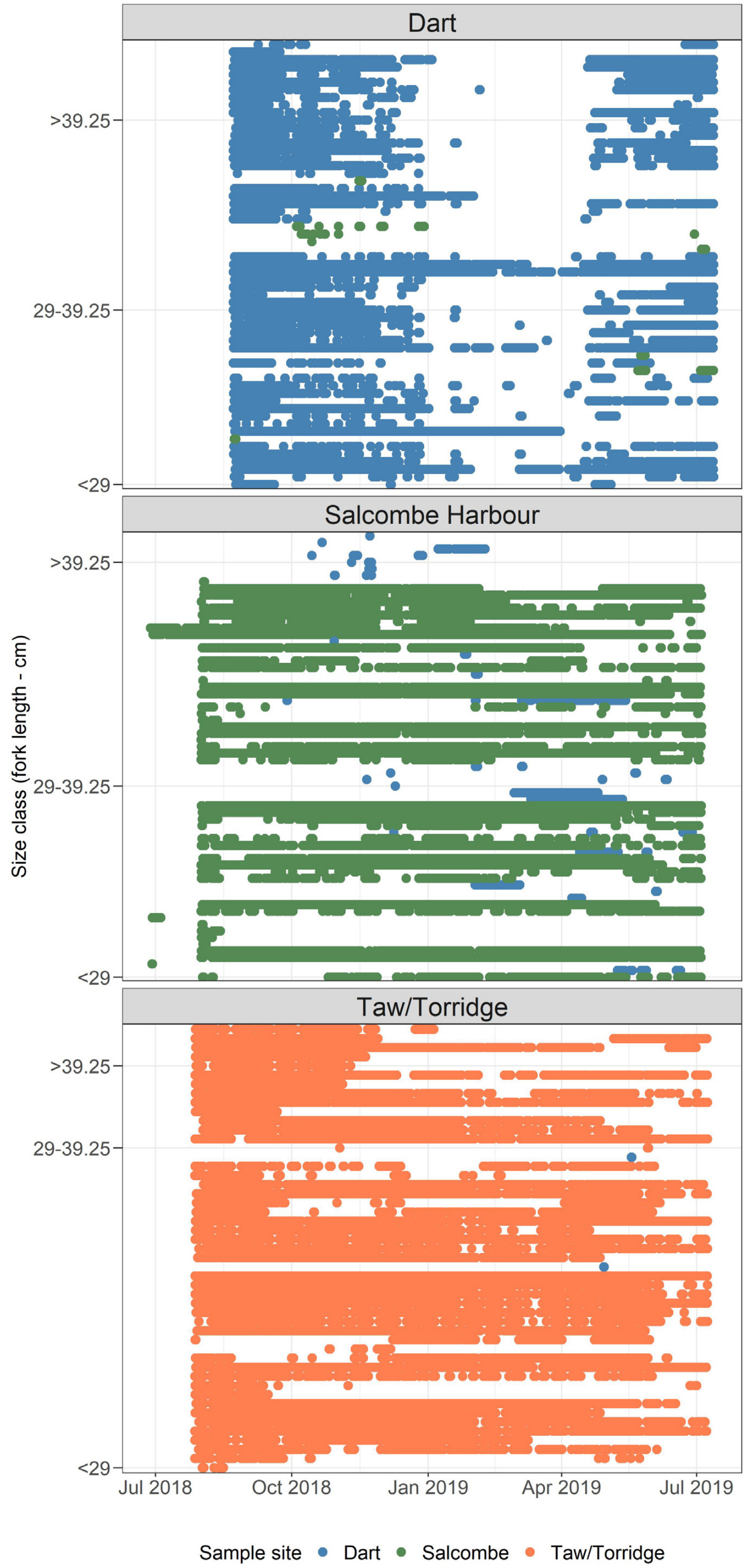

Figure 4. Abacus plot displaying detections of tagged fish by date/time. Each row represents an individual fish. The nursery site each fish was tagged within colour coded. Fish arranged in ascending size order. Size classes identified by Pickett and Pawson (1994): < 29 cm fork length: Juvenile, 29–39.25 cm fork length: Adolescent, and > 39.25 cm fork length: Adult.

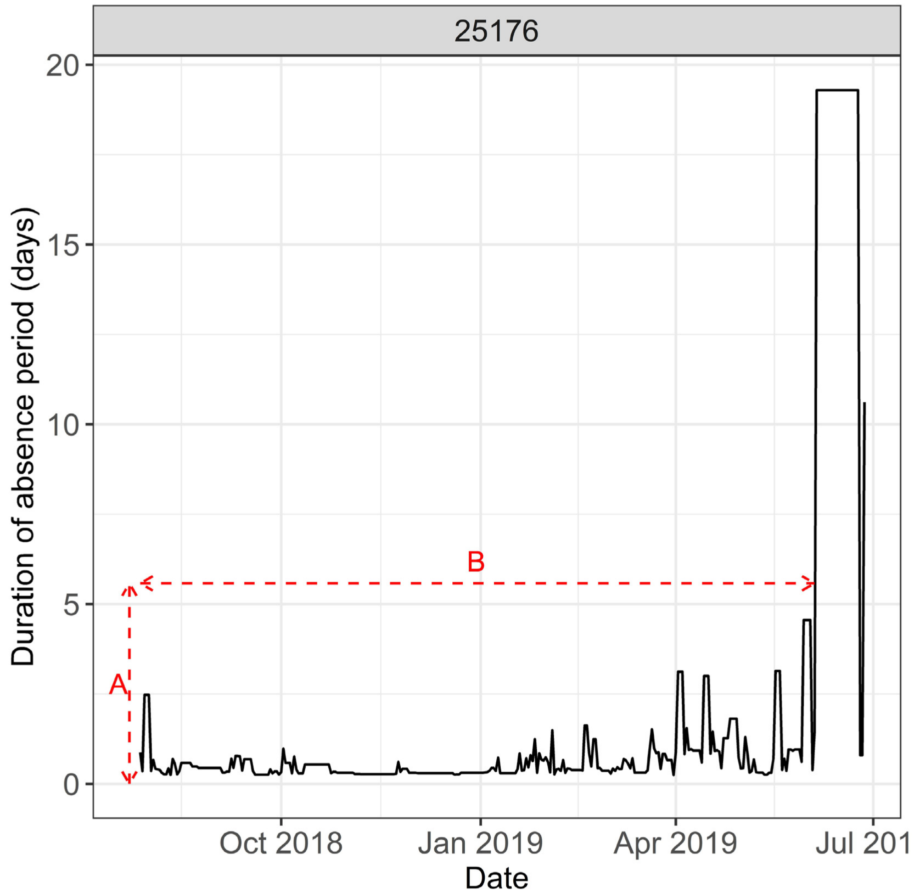

Figure 5. Example time series of absence periods for tag ID 25176. Arrow A indicates the duration of individual absence periods. Arrow B indicates the duration of time Tagging Site Residence is sustained.

Table 2. Candidate linear models to test the effect of nursery site and fork length on Tagging Site Residence. Models ranked according to ΔAIC scores. Selected model emboldened.

Model ID	Model notation	Δ AIC
M_{TSR3}	***Tagging site residence (% of tracking period) ∼ Nursery site***	**0**
M_{TSR2}	*Tagging site residence (% of tracking period) ∼ Nursery site + Fork length*	2.29
M_{TSR1}	*Tagging site residence (% of tracking period) ∼ Nursery site ∗ Fork length*	6.29
M_{TSR4}	*Tagging site residence (% of tracking period) ∼ Fork length*	33.58
M_{TSR5}	*Null model (no fixed effects)*	32.65

estuaries—six fish). These fish had an average length of 32.2 cm (Range: 25.3–60 cm, IQR: 28.8–37.4 cm), and these suspected migrations had an average duration of 118.2 d (Range 50–296 d, IQR: 79.8–142 d). A total of 25% of the fish departed by 31/12/2018, the median departure date was 14/02/2019, and 75% had departed by: 26/03/2019. 49 out of the 60 (81%) fish that made these suspected migrations returned to the original site in which they were tagged. 25% of these fish had returned by 15/05/2019, the median return date was 25/06/2019, and 75% had returned by: 13/08/2019.

The remaining 73 fish (55%; Dart estuary—12, Salcombe harbour—27, and Taw/Torridge estuary—34), were detected in their respective nursery sites throughout the winter (representative example demonstrated in Figure 2; tag ID 25131). These fish had an average length of 30.8 cm (Range: 25.5–52 cm, IQR: 27.9–32.4 cm).

Tagging site residence

Tagging Site Residence (TSR) is a combination of: (1) the duration of time fish were within each nursery site (defined as "residence periods"), and (2) the duration of time fish made relatively short absence periods from each nursery site (defined as "coastal movement"). This provided an estimate of how long each fish was either within or in close proximity to each nursery site.

A total of 18 526 residence periods were detected, with an average of 139.3 residence periods per fish (Range: 3–444, IQR: 57–208), which had an average duration of 0.6 d (Range: 0.1–2, IQR:

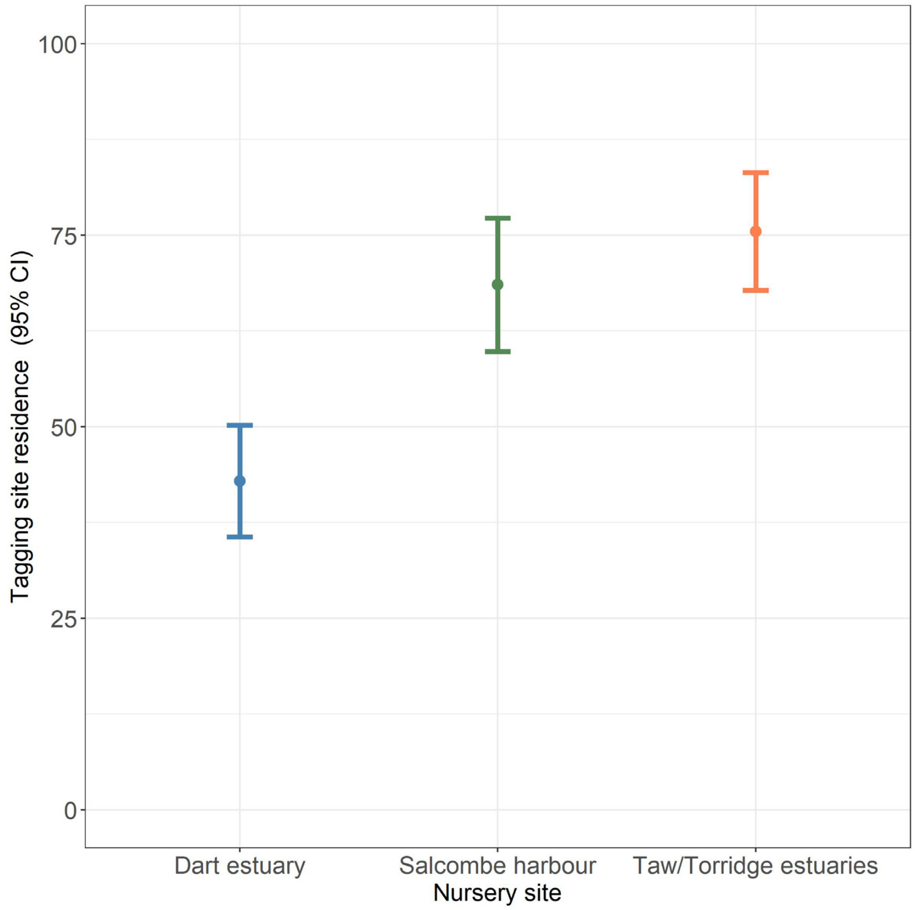

Figure 6. Predicted Tagging Site Residence (± 95% *CI*) of European bass from nursery sites: Dart estuary, Salcombe harbour, and Taw/Torridge estuaries.

Table 3. Linear model coefficients for M_{TSR3}, testing differences in TSR between nursery sites.

	Coefficient	Estimate	Std. Error	*T* value	*p*
Nursery site	Intercept (Dart estuary)	42.889	3.691	11.619	< 0.001
	Salcombe harbour	25.628	5.738	4.466	< 0.001
	Taw/Torridge estuary	32.598	5.360	6.082	< 0.001

0.1–0.5). Once the splitting rules derived from the PELT tree classification method were applied to the data, 129 out of 133 tagged fish were identified as exhibiting absence periods which were defined as "coastal movement" (Dart estuary: 50; Salcombe harbour: 35; and Taw/Torridge estuaries: 46). During segments of time when fish displayed "coastal movement" individual absence periods had an average duration of 0.9 d (Range: 0.3–6.2 d, IQR: 0.4–1 d), and this behaviour was sustained for an average period of 36.6 d (Range: 0–337 d, IQR: 5–26 d; Figure 5).

Linear modelling suggested that TSR varied between nursery sites, however fork length was not a significant predictor (Table 2; Linear model—Adj.R^2: 0.23, $F_{2,130}$: 20.45, $p < 0.001$).

TSR within the Dart estuary was 42.89% and was significantly lower than in the Taw/Torridge estuaries and Salcombe harbour (Range: 10.22–98.16%, IQR: 26.11–56.91; Tukey test: Dart–Salcombe, $p = \leq 0.001$; Tukey test Taw/Torridge–Dart, $p = \leq 0.001$). No difference was detected between Salcombe harbour and the Taw/Torridge estuaries (Tukey test: $p = 0.46$) in which TSR was 68.52% (Range: 0.19–99.6%, IQR: 42.29–94.76) and 75.49% (Range: 0.02–99.1%, IQR: 63.92–94.6%; Figure 6 and Table 3).

Calculating coastal ROM

During periods of "Wider movement," 35 fish were detected in locations outside of the nursery site in which they were tagged (78 837 detections). A total of 24 fish tagged within the Dart estuary were detected within Salcombe harbour, and eight fish tagged in Salcombe harbour were detected in the Dart estuary (24.9 km straight-line distance). Three fish tagged in the Taw/Torridge estuary were detected by a receiver array within Swansea Bay and the Gower peninsula, Wales, operated by Swansea University (66.1–72.9 km straight-line distance). In total, two fish tagged in the Dart estuary were detected in the Taw/Torridge estuary via Salcombe harbour (312 km straight-line distance; Figure 7). Due to the high distance

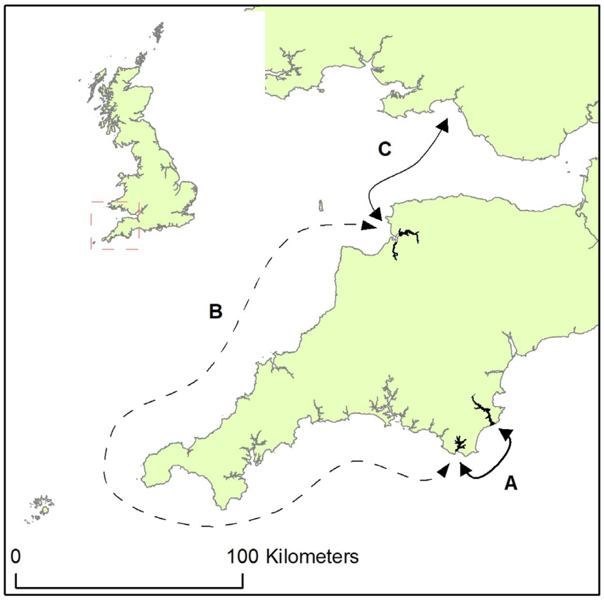

Figure 7. Coastal fish movement. Arrow A: Dart estuary–Salcombe harbour (length = 24.9 km), Arrow B: Salcombe harbour–Taw/Torridge estuaries (length = 317 km), and Arrow C: Taw/Torridge estuaries–Swansea bay/Gower Peninsula (length = 66.1–72.9 km). Solid arrows indicate movement included in coastal ROM calculations, arrow B not included.

Table 4. Table of coefficients for generalized linear model (Family = Gaussian, link = log): ROM ~ Fork length.

Coefficients	Estimate	Standard error	*T* value	*p*
Intercept	− 3.749	0.321	− 11.663	< 0.001
Fork length	0.036	0.006	5.935	< 0.001

between Salcombe harbour and the Taw/Torridge estuaries, and the likelihood of meandering or erratic movement trajectories creating inaccurate ROM estimations, these movements were not included within coastal ROM calculations.

When combined with individual ROM estimates within O'Neil (2017), a significant positive relationship was found between coastal ROM and fork length (Table 4).

Estimating dispersal distances from nursery sites

To meet the assumptions of normality and homogeneity of variance a log transformation was applied to the estimated range values. M_{disp2} was the best fitting model for predicting dispersal distance, this included nursery site and fork length with no interaction term (Table 5). Inclusion of the AR(1) correlation structure reduced M_{disp2} Δ AIC scores by 426.5, highlighting the model fit was greatly improved by accounting for the temporal dependency structure of the data. Furthermore no significant temporal autocorrelation was visually apparent within ACF plots following inclusion of the AR(1) correlation structure.

M_{disp2} predicted that dispersal distance increased log linearly with fork length and significantly differed between the Dart and Taw/Torridge estuaries, and, Salcombe harbour (Tukey test: Dart–Salcombe, $p = 0.002$; Dart–Taw/Torridge, $p = 0.924$; and Salcombe–Taw/Torridge, $p \leq 0.001$; Table 6 and Figure 8).

Following a back calculation, random effect estimates from M_{disp2} (Figure 8B) indicate that across the length range included within the study (25.3–60 cm fork length) dispersal distance varied from 2.4 to 20.1 km. When using the median fish length (29.8 cm fork length), fish dispersed to an estimated distance of 4.5 km (± 2.4 km 95% *CI*) from the Dart estuary, 3.7 km (± 2.9 km 95% *CI*) from Salcombe harbour, and 4.6 km (± 3.5 km 95% *CI*) from the Taw/Torridge estuaries (Figures 8 and 9).

Discussion

The high temporal and spatial resolution of the acoustic telemetry data presented here demonstrates the complexity of juvenile and sub-adult European bass movements within coastal environments. Tagged fish displayed high residency to the nursery site in which they were fist tagged and made repeated short-range movements within and adjacent to site boundaries. Fish were however also recorded making long-range movements, which ranged from 24.9 to 312 km.

Essential fish habitat

In the current study, a range of fish sizes were tagged (25.2–60 cm fork length), which includes; juveniles, sub-adult, and sexually mature fish (Pickett and Pawson, 1994). Across this size range, length did not predict the cumulative duration of time fish spent within or in close proximity to the nursery sites; this suggests that estuaries and shallow embayments (plus the associated habitats e.g. saltmarsh or rocky reefs) are important for European bass across a range of different life stages. As evidenced with similar and sympatric species (e.g. Striped bass *Morone saxatilis*; Ng *et al.*, 2007; Baker *et al.*, 2016 and Thinlip grey mullet *Chelon ramada;* Laffaille *et al.*, 2002), whilst occupying coastal sites resident European bass populations may be reliant on the local availability of habitats and prey species for: nutrition, growth, and ultimately survival (Pickett and Pawson, 1994; Cambie *et al.*, 2016; Doyle *et al.*, 2017).

Furthermore, 55% (73 out of 133) of tagged fish within the current study were not absent from their respective nursery site for any period greater than 6.2 d throughout winter. During winter, European bass are thought to be mostly absent from coastal sites in the UK (Pickett and Pawson, 1994), when they either conduct spawning migrations or seek thermal refuge in deeper offshore water (Pickett and Pawson, 1994). The overwintering fish detected in this study ranged in fork length from 25.5 to 60 cm, and therefore represent both overwintering sub-adults and sexually mature fish, which may have skipped a spawning migration (Pickett and Pawson, 1994; O'Neill, 2017). Sympatric taxa such as Grey Mullet (*Chelon spp.*) or Gilthead bream (*Sparus aurata*) are similarly thought to occupy coastal sites during the summer/autumn however during winter are largely absent (Laffaille *et al.*, 2002; Maes *et al.*, 2007; Mercier *et al.*, 2012). The evidence reported here, may therefore be due to a prior gap in understanding European bass (or wider fish behaviour—Marsden *et al.*, 2021) during winter, or an indication of behavioural plasticity as a response to environmental and/or site specific conditions. This data however does highlight that not all European bass migrate or move offshore in the winter, and that estuaries, embayments and coastal waters can remain highly utilized throughout the year.

Table 5. Candidate linear mixed effect models to test the effect of nursery site and fork length on European bass dispersal distance. Models ranked according to delta AIC scores. Selected model emboldened.

Model ID	Model notation	Δ AIC
M_{disp2}	***Dispersal distance ∼ Nurserysite + Fork length***	**0**
M_{disp4}	*Dispersal distance ∼ Fork length*	6.72
M_{disp1}	*Dispersal distance ∼ nursery site ∗ Fork length*	16.51
M_{disp3}	*Dispersal distance ∼ nursery site*	72.43
M_{disp5}	*Null model (no fixed effects)*	74.41

Table 6. Fixed and random effects of the linear mixed effect model estimating European bass dispersal distance in relation to nursery site and fork length.

Fixed effects	Estimate	Std. Error	95% *CI* Lower	95% *CI* upper	*T* value	*p* value
Nursery site: Dart (Intercept)	7.131	0.139	6.858	7.403	51.232	< 0.001
Nursery site: Salcombe	− 0.197	0.055	− 0.307	− 0.087	− 3.549	< 0.001
Nursery site: Taw/Torridge	0.026	0.052	− 0.077	0.129	0.494	0.621
Fork length	0.041	0.004	0.033	0.049	10.277	< 0.001
Random effects						
Tag ID	0.222					
Residual	0.651					

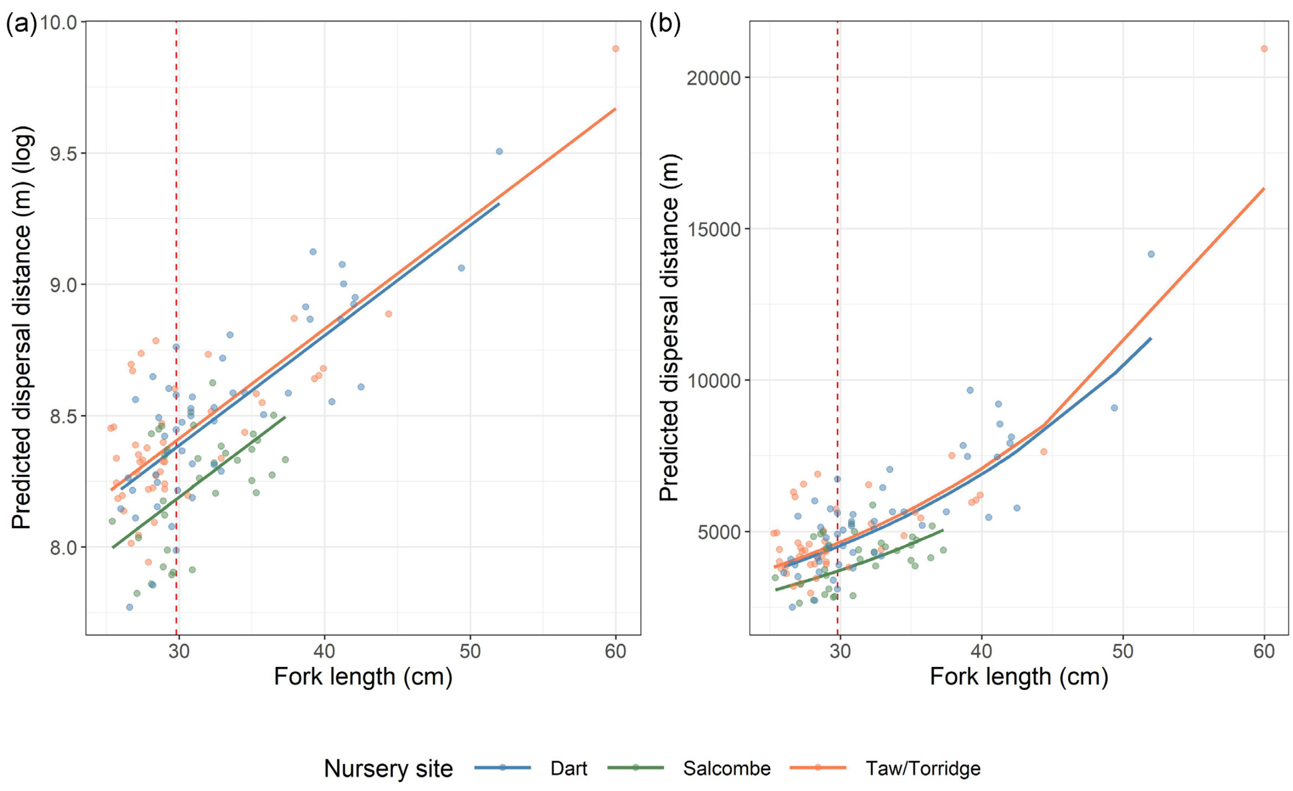

Figure 8. (A) Log transformed predicted European bass dispersal distance: Dart estuary, Salcombe harbour, and Taw/Torridge estuaries during Tagging Site Residence. (B) Back transformed predicted European bass dispersal distance. Colour coded lines represent model fits for each nursery site, points represent random effect coefficients (i.e. individual fish). Red dashed line indicates median fish length included within the study (29.8 cm fork length).

Estuaries and the habitats they encompass are however highly influenced by anthropogenic activities (Laffaille *et al.*, 2001; Kennish, 2002; Lotze *et al.*, 2006; Vasconcelos *et al.*, 2007). The loss or degradation of estuarine habitats can therefore result in a substantial declines in local fish populations (e.g. 66% loss—MClusky *et al.*, 1992 and 23% loss—Rochette *et al.*, 2010). This is particularly problematic as it is estimated that 85% of coastline across Europe is at high or moderate risk for unsustainable coastal construction and

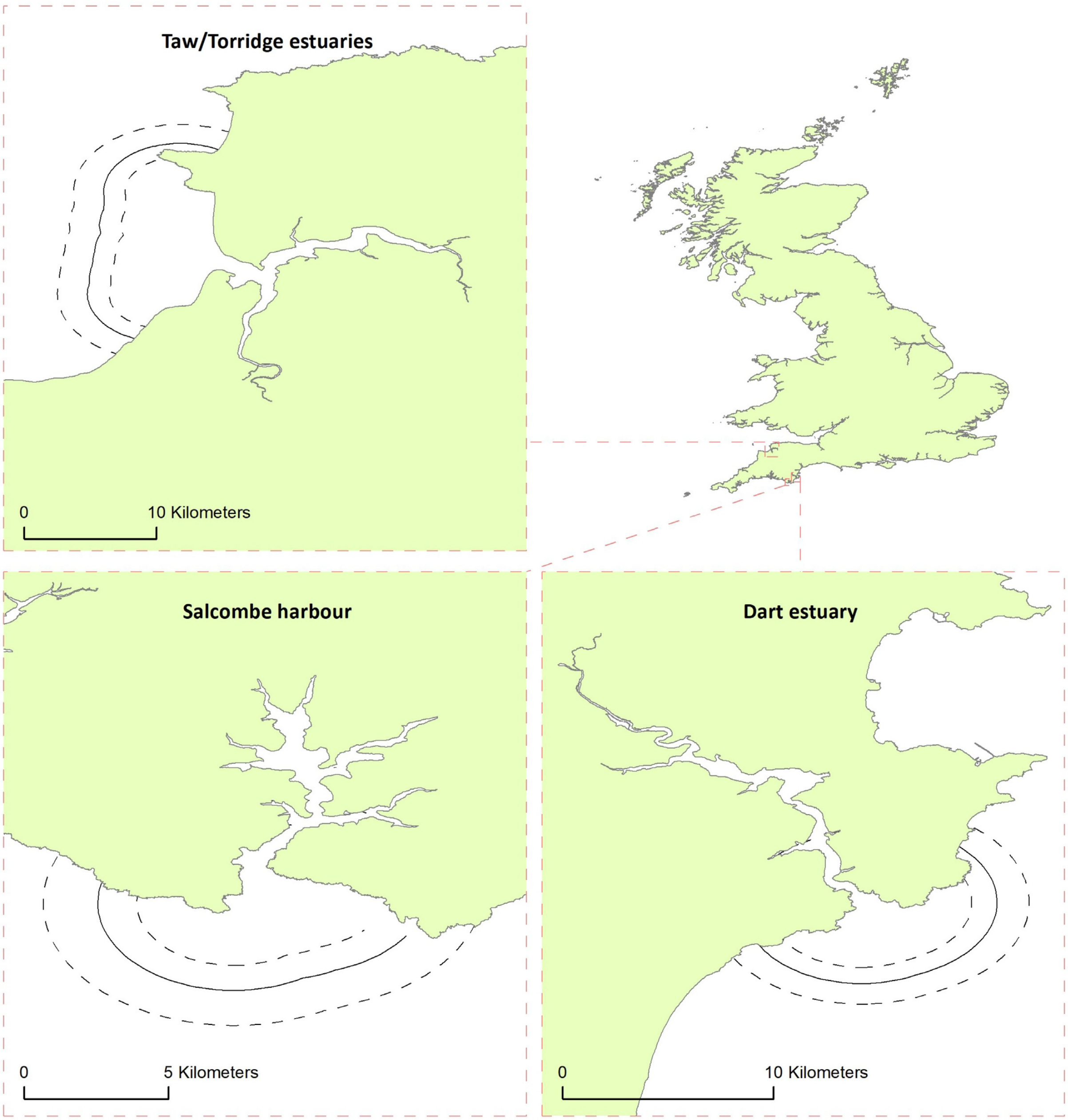

Figure 9. Estimated dispersal distance of European bass from nursery sites during periods of "Tagging site residence." Estimate based on median fish size tagged: 29.8 cm fork length. Solid line represents exponent of model intercept and dashed lines represent exponent of 95% *CI*. Please refer to Table 6 for model outputs and coefficients.

development (Seitz *et al.*, 2014). Therefore, if increasing recruitment and survivorship within coastal sites is a recovery objective for Northern European bass stock, the merits of further human activities which are likely to negatively impact estuarine or coastal environments e.g. coastal land development (Laffaille *et al.*, 2000), should be considered in relation to the associated impact on fish populations.

Due to the high residency reported here, the authors suggest that estuarine and coastal nursery sites should be defined as "Essential Fish Habitat" as listed in the Magnuson–Stevens Fishery Act (2007). Within the context of the highly impoverished condition of the Northern European bass stock, habitats which have been identified as "Essential" should be included within Marine Spatial Planning and/or protected through legislative instruments within the Reformed Common Fisheries Policy or the UK Fisheries Bill e.g. Fish Stock Recovery areas (Cambiè *et al.*, 2016; Doyle *et al.*, 2017; Dambrine *et al.*, 2020).

Local movements

Within the current study juvenile and sub-adult fish were only predicted to move within an area of 2.4–20.1 km, from the coastal nursery site they were tagged, for a 42.9–75.5% of the year. This behaviour may introduce spatial structuring, in which local processes may affect local juvenile/sub-adult survival rates. Site-specific environmental conditions and local human activities could result in variability in local population abundances (Laffaille *et al.*, 2000; Ciannelli *et al.,* 2013; Neat *et al.*, 2014), which if not researched further could lead to an inaccurate understanding of local fish population stressors (Ying *et al.*, 2011). Furthermore, European bass settlement within coastal nursery sites may follow stochastic processes, which when combined with the slow growth rate of this species e.g. sexually maturity achieved in 4–7 years, could result in a protracted recovery (several years) if local European bass populations become depleted (Pickett and Pawson, 1994; Pickett *et al.*, 2004). If not reflected in management actions, this could complicate European bass recovery efforts and have substantial impacts on the resilience of the wider population (Pickett *et al.*, 2004; Ciannelli *et al.*, 2013; Neat *et al.*, 2014).

Some individuals were however also detected making long-range movements to other coastal sites e.g. between Dart estuary and South Wales (312 km). This may be evidence of adolescent fish seeking feeding sites, which they will adopt as sexually mature fish and could be a behavioural adaptation to allow greater dispersal along the coastline (Pickett and Pawson, 1994). The significant differences in the duration of time fish displayed residency to nursery sites reported here, however also suggests that local conditions rather than size/maturation are important drivers for local fish behaviour (Pickett and Pawson, 1994). This has similarly been evidenced within other estuarine fish species e.g. Spotted grunter (*Pomadasys commersonnii*—Childs *et al.*, 2008), the movements of which are correlated with local fluctuations in salinity, water temperature and turbidity. Furthermore, 81% of the fish that made long-range movements returned to the same location after 3–4 months. These results therefore suggest that despite some fish making long-range movements, European bass display high site fidelity at a juvenile/sub adult stage and that local conditions may be important drivers for dispersal into the wider coastline.

Spatial management

All the nursery sites included within the current study are designated as Bass Nursery Areas (BNA), this is a form of spatial management in which targeted commercial fishing for European bass is seasonally prohibited within site boundaries. While the effectiveness of BNA has yet to be formally assessed, Pickett *et al.* (2004) argued they likely increase local recruitment to commercial and recreational fisheries. Further work should be conducted to assess the benefits of spatial management for this species. However, the restricted movement patterns identified within the current study and those reported within the wider literature (Green *et al.*, 2012; Cambiè *et al.*, 2016; Doyle *et al.*, 2017; Pontual *et al.*, 2019) support the efficacy of spatial management strategies such as BNAs.

Conclusions

This study is the first to document juvenile and sub-adult European bass movement characteristics at a high temporal and spatial resolution. The sites selected within the current study varied in spatial extent (Dart: 8.32 km^2, Salcombe harbour: 6.34 km^2, and Taw/Torridge estuaries: 14.6 km^2), but are typical examples of estuaries and ria systems across Europe. The results presented are therefore likely to be representative of juvenile/sub adult European bass behaviour more broadly across Northern Europe.

As part of the UK Government (UK Fisheries Act, 2020) and European Commission's (Marine Strategy Framework Directive) target for Good Environmental Status (GES), populations of all commercially exploited fish should be within "safe biological limits." The results presented here suggest that, recognition of the habitat requirements for, and the movement characteristics of, European bass would contribute towards GES as well as support the recovery of one of Europe's most valuable commercial and recreational fisheries.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data availability statement

The data underlying this article will be shared on reasonable request to the corresponding author.

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References

Baker, H. K., Nelson, J. A., and Leslie, H. M. 2016. Quantifying striped bass (*Morone saxatilis*) dependence on saltmarsh-derived productivity using stable isotope analysis. Estuaries and Coasts, 39: 1537–1542.

Bégout Anras, M. L., Covés, D., Dutto, G., Laffargue, P., and Lagardère, F. 2003. Tagging juvenile seabass and sole with telemetry transmitters: medium-term effects on growth. ICES Journal of Marine Science, 60: 1328–1334.

Cambiè, G., Kaiser, M. J., Marriott, A. L., Fox, J., Lambert, G., Hiddink, J. G., Overy, T. *et al.* 2016. Stable isotope signatures reveal small-scale spatial separation in populations of European sea bass. Marine Ecology Progress Series, 546: 213–223.

Campbell, H. A., Watts, M. E., Dwyer, R. G., and Franklin, C. E. 2012. V-Track: software for analysing and visualising animal movement from acoustic telemetry detections. Marine and Freshwater Research, 63: 815–820.

Childs, A.-R., Cowley, P., Næsje, T., Booth, A., Potts, W., Thorstad, E., and Økland, F. 2008. Do environmental factors influence the movement of estuarine fish? A case study using acoustic telemetry. Estuarine, Coastal and Shelf Science 78: 227–236.

Ciannelli, L., Fisher, J. A., Skern-Mauritzen, M., Hunsicker, M. E., Hidalgo, M., Frank, K. T., and Bailey, K. M. 2013. Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes: a review. Marine Ecology Progress Series, 480: 227–243.

Dambrine, C., Woillez, M., Huret, M., and De Pontual, H. 2020. Characterising essential fish habitat using spatio-temporal analysis of fishery data: a case study of the European seabass spawning areas. Fisheries oceanography, 30: 413–428. doi: 10.1111/fog.12527.

Doyle, T. K., Haberlin, D., Clohessy, J., Bennison, A., and Jessopp, M. 2017. Localised residency and inter-annual fidelity to coastal foraging areas may place sea bass at risk to local depletion. Scientific reports, 7: 45841.

D&S IFCA. 2018. Netting Permit Byelaw D&S IFCA Authority. url: Netting Permit Byelaw

European Market Observatory for Fisheries and Aquaculture Products (EUMOFA). 2020. Commercial and recreational fisheries for wild seabass in the Atlantic, Economic and market study. doi: 10.2771/652840. url: EUMOFA Publications Office of the European Union, Luxembourg.

Green, B. C., Smith, D. J., Grey, J., and Underwood, G. J. 2012. High site fidelity and low site connectivity in temperate salt marsh fish populations: a stable isotope approach. Oecologia, 168: 245–255.

ICES. 2020. Sea bass (Dicentrarchus labrax) in divisions 4.b–c, 7.a, and 7.d–h (central and southern North Sea, Irish Sea, English Channel, Bristol Channel, and Celtic Sea). doi: doi.org/10.17895/ices.advice.5916 In Report of the ICES Advisory Committee

Kelley, D. 1988. The importance of estuaries for sea-bass, *Dicentrarchus labrax* (L.). Journal of Fish Biology, 33: 25–33.

Kennish, M. J. 2002. Environmental threats and environmental future of estuaries. Environmental Conservation, 29: 78–107.

Killick, R., and Eckley, I. 2014. changepoint: an R package for changepoint analysis. Journal of Statistical Software, 58: 1–19.

Laffaille, P., Feunteun, E., Lefebvre, C., Radureau, A., Sagan, G., and Lefeuvre, J.-C. 2002. Can thin-lipped mullet directly exploit the primary and detritic production of European macrotidal salt marshes? Estuarine, Coastal and Shelf Science, 54: 729–736.

Laffaille, P., Lefeuvre, J.-C., and Feunteun, E. 2000. Impact of sheep grazing on juvenile sea bass, *Dicentrarchus labrax* L., in tidal salt marshes. Biological Conservation, 96: 271–277.

Laffaille, P., Lefeuvre, J.-C., Schricke, M.-T., and Feunteun, E. 2001. Feeding ecology of o-group sea bass, *Dicentrarchus labrax*, in salt marshes of Mont Saint Michel Bay (France). Estuaries, 24: 116–125.

Lefrancois, C., Odion, M., and Claireaux, G. 2001. An experimental and theoretical analysis of the effect of added weight on the energetics and hydrostatic function of the swimbladder of European sea bass (Dicentrarchus labrax). Marine Biology, 139: 13–17.

Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., Kidwell, S. M. *et al.* 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science, 312: 1806–1809.

Madon, B., and Hingrat, Y. 2014. Deciphering behavioral changes in animal movement with a “multiple change point algorithm-classification tree”framework. Frontiers in Ecology and Evolution, 2: 30.

Maes, J., Stevens, M., and Breine, J. 2007. Modelling the migration opportunities of diadromous fish species along a gradient of dissolved oxygen concentration in a European tidal watershed. Estuarine, Coastal and Shelf Science 75: 151–162.

MAFF. 1990. Bass Nursery Areas and other conservation measures. url: MAFF - BNA

Marsden, J., Blanchfield, P., Brooks, J., Fernandes, T., Fisk, A., Futia, M., Hlina, B. *et al.* 2021. Using untapped telemetry data to explore the winter biology of freshwater fish. Reviews in Fish Biology and Fisheries, 31: 1–20.

McLusky, D. S., Bryant, D. M., and Elliott, M. 1992. The impact of land-claim on macrobenthos, fish and shorebirds on the forth estuary, eastern Scotland. Aquatic Conservation: Marine and Freshwater Ecosystems, 2: 211–222.

Mercier, L., Mouillot, D., Bruguier, O., Vigliola, L., and Darnaude, A. M. 2012. Multi-element otolith fingerprints unravel sea— lagoon lifetime migrations of gilthead sea bream Sparus aurata. Marine Ecology Progress Series, 444: 175–194.

MMO. 2020. UK Sea fishing Statistics. Available at: https://www.gov.uk/government/collections/uk-sea-fisheries-annual-statistics (Last accessed date: 09/09/2021).

Neat, F. C., Bendall, V., Berx, B., Wright, P. J. Ó., Cuaig, M., Townhill, B., Schön, P. J. *et al.* 2014. Movement of Atlantic cod around the British Isles: implications for finer scale stock management. Journal of Applied Ecology, 51: 1564–1574.

Ng, C. L., Able, K. W., and Grothues, T. M. 2007. Habitat use, site fidelity, and movement of adult striped bass in a southern New Jersey estuary based on mobile acoustic telemetry. Transactions of the American Fisheries Society, 136: 1344–1355.

O'Neill, R. 2017. The Distribution of the European Sea Bass, Dicentrarchus labrax, in Irish waters. University College Cork. University College Cork, Ireland.

Pawson, M., Pickett, G., and Kelley, D. 1987. The distribution and migrations of bass, *Dicentrarchus labrax* L., in waters around England and Wales as shown by tagging. Journal of the Marine Biological Association of the United Kingdom, 67: 183–217.

Pickett, G., Kelley, D., and Pawson, M. 2004. The patterns of recruitment of sea bass, *Dicentrarchus labrax* L. from nursery areas in England and Wales and implications for fisheries management. Fisheries Research, 68: 329–342.

Pickett, G., and Pawson, M. 1994. Sea Bass: Biology, Exploitation and Conservation, Chapman & Hall, United Kingdom.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and Team, R. C. 2019. Linear and nonlinear mixed effects models. R Package Version, 3: 1–89.

Pontual, H., Lalire, M., Fablet, R., Laspougeas, C., Garren, F., Martin, S., Drogou, M. *et al.* 2019. New insights into behavioural ecology of European seabass off the West Coast of France: implications at local and population scales. ICES Journal of Marine Science, 76: 501–515.

Ripley, B., 2019. Package 'tree'. Classification and Regression Trees. Version: 1.0–36. CRAN R-project:tree

Rochette, S., Rivot, E., Morin, J., Mackinson, S., Riou, P., and Le Pape, O. 2010. Effect of nursery habitat degradation on flatfish population: application to Solea solea in the Eastern Channel (Western Europe). Journal of Sea Research, 64: 34–44.

R core team. 2019. R: a language and environment for statistical computing; 2015. R-project

Seitz, R. D., Wennhage, H., Bergström, U., Lipcius, R. N., and Ysebaert, T. 2014. Ecological value of coastal habitats for commercially and ecologically important species. ICES Journal of Marine Science, 71: 648–665.

Vasconcelos, R., Reis-Santos, P., Fonseca, V., Maia, A., Ruano, M., França, S., Vinagre, C. *et al.* 2007. Assessing anthropogenic pressures on estuarine fish nurseries along the Portuguese coast: a multimetric index and conceptual approach. Science of the Total Environment, 374: 199–215.

Wright, P., Christensen, A., Régnier, T., Rindorf, A., and van Deurs, M. 2019. Integrating the scale of population processes into fisheries management, as illustrated in the sandeel, ICES Journal of Marine Science, 76: 1453–1463.

Wright, P. J., Doyle, A., Taggart, J., and Stirling, A. 2020. Linking scales of life-history variation with population structure in Atlantic cod. Frontiers in Marine Science, 8: 630515.

Ying, Y., Chen, Y., Lin, L., and Gao, T. 2011. Risks of ignoring fish population spatial structure in fisheries management. Canadian Journal of Fisheries and Aquatic Sciences, 68: 2101–2120.

Zuur, A. F., Hilbe, J., Ieno, E. N., Zuur, A., Hilbe, J., and Leno, E. 2013. A Beginner's Guide to GLM and GLMM with R: A Frequentist and Bayesian Perspective for Ecologists, Highland Statistics Limited, United Kingdom.

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